

Form and Motion of *Donax variabilis* in Flow

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Abstract. The coquina clam, *Donax variabilis*, rides flow from waves, migrating shoreward during rising tides and seaward during falling tides. This method of locomotion, swash-riding, is controlled not only behaviorally but also morphologically. The shape of this clam causes it to orient passively: a clam rotates in flow, usually in backwash, until its anterior end is upstream. Rotation is about a vertical axis through a pivotal point where the shell touches the sand. The density, weight distribution, and wedge-like shape are all important in effecting orientation. Such orientation is significant because it contributes to stability of motion. On an unoriented clam, upward lift can be higher than its underwater weight—a circumstance that results in uncontrollable tumbling. In contrast, once oriented with its anterior end upstream, a clam experiences downward lift that contributes to its stability while sliding in backwash. Furthermore, when the anterior end is upstream, drag is reduced relative to when the ventral, dorsal, or posterior ends are upstream. Since orientation occurs only above a minimum velocity, it has the effect of slowing a clam's motion over the substratum in rapid flows. Stability, drag, and speed reduction enhance a clam's ability to gain a foothold and dig in after a swash-ride, before wave flows can wash it off the beach and out to sea.

Introduction

The coquina clam, *Donax variabilis*, migrates seaward with the falling tide and shoreward with the rising tide by using a method of locomotion called swash-riding (Ellers, 1987, 1988). Swash-riding involves jumping out of the sand, being pushed by a wave to a new location, and digging in again. For an individual clam, the net movement per swash-ride depends in part on behavior. For instance,

by using sound to sense the size and timing of incoming waves (Ellers, 1995b), these clams emerge to ride only the largest waves (Ellers, 1995a). The net movement per swash-ride may also depend on a clam's shape, just as shape has consequences for performance in other forms of locomotion such as running or flying.

Consider events during a shoreward migration consisting of several swash-rides. During each swash-ride, a clam is pushed shoreward, but does not stop moving at the most shoreward point of its travel because backwash pulls it seaward. To make net shoreward progress, it must gain a foothold while moving and dig in before backwash carries it seaward of its original position. How far flow moves a clam and whether it gains a foothold depend on forces the clam experiences in flow, which in turn depend on the clam's shape. The present study seeks to identify shape, or form, that influences the motion of a swash-riding clam.

The motion of an object in flow can be of two dramatically different types. An object can orient to a stable position like a weather vane or it can tumble chaotically like a hat. A *D. variabilis* clam moves like a weather vane. If the water flowing past an individual *D. variabilis* changes direction, the clam rotates to maintain a certain orientation with respect to flow (Fig. 1). The clam rotates about a vertical axis through a pivotal point where the shell touches the sand. In the oriented position, the clam's anterior end is upstream and the posterior end is downstream. Once oriented, a clam slides stably before gaining a foothold and digging into the sand (Fig. 2).

This orientation was suggested to be caused by activity of the siphons in *D. fossor* (Jacobson, 1955) and in *D. semigranosus* (Mori, 1938). However, dead *D. denticulatus* (Wade, 1967) and dead *D. variabilis* (Tiffany, 1971; Ellers, 1987, 1988) orient the same way as live ones, thus demonstrating the passive nature of orientation.

Not every shape orients and slides stably in backwash. For example, a bivalve, the cross-hatched lucine *Divari-*

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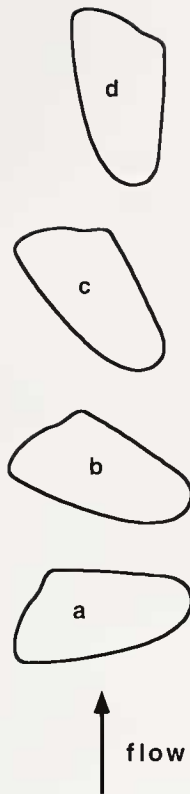


Figure 1. A coquina clam, *D. variabilis*, orienting passively in flow. A clam starts out in an arbitrary position, e.g., ventral edge upstream (a). In flow it rotates, passing through positions (b) and (c) until it reaches the stable orientation with the anterior end upstream (d). Orientation is rapid and can occur during <0.1 s. The clam may slide downstream during orientation, as shown, or remain stationary while rotating.

cella quadrisculata, stands on edge and rolls like a wheel (pers. obs.). Another bivalve, the sunray Venus *Macrocallista nimbosa*, slides in a variety of orientations and tumbles occasionally. A very light bivalve, the tellin *Tellina iris* tumbles chaotically. A sand dollar, *Mellita quinquesperforata*, flips end over end in surf. Similar characteristic motions of these objects occur in a flow tank. Therefore, orientation by *D. variabilis* is a special consequence of the shape of *D. variabilis*, not a general characteristic of bivalves or other invertebrates that live exposed to flow.

Furthermore, orientation is common among swash-riding species. Among the swash-riding gastropods and mole crabs for which information is available, all orient (Ellers, 1987). Other swash-riders include a variety of amphipods, but observations of orientation are unavailable for those species.

Orientation in *D. variabilis* usually occurs in the backwash rather than the swash, presumably because flow in the swash is too turbulent. Swash forms from a collapsing bore that itself originates from a breaking wave. The speeds

of resulting flows are relevant to the fluid dynamics of a swash-riding clam. The speed of the leading edge of swash initially increases, then decreases as it moves shoreward. Maximum speeds (Bradshaw, 1982) ranged from 4.5 to 6 m s^{-1} from waves with breaker heights of 0.9 to 1.4 m on a steeply sloped beach (slope expressed as rise-to-run ratio was 0.16); and the maximum speed recorded on a shallow beach (slope of 0.03), where bore collapse takes longer, was 3 m s^{-1} . Backwash speed is typically less than swash speed. Maximum backwash speed, just shoreward of the next incoming bore, was 1.2 m s^{-1} on a beach with slope of 0.03 (Bradshaw, 1982). The average speed was 0.70 m s^{-1} among 21 backwashes. Backwash generally increases in speed as it flows seaward. I observed *D. variabilis* riding flows on beaches typically having a slope of 0.1 , but varying from 0.05 at low tide to 0.13 at high tide.



Figure 2. Coquina clams, *D. variabilis*, in flow on a beach. Flow is from upper right to lower left and is indicated by the streaks from the moving bubbles on the surface of the water. The upper photo shows clams swash-riding and oriented with the anterior end upstream. The lower photo shows a clam on a beach, having just achieved a foothold, shortly before it burrows into the sand. The foot is visible at the pointy, anterior end, and the siphons are visible at the blunt, posterior end.

This study seeks to determine morphological features of *D. variabilis* that are important in causing orientation; and to determine the functional consequences of orientation for movement of *D. variabilis* during swash-riding. Relevant are forces and moments of forces due to friction between clam and sand; gravity; buoyancy; drag; vertical and horizontal lifts (lift is defined as a force normal to flow, and there are always two mutually perpendicular lift vectors normal to the flow direction). By combining measurements and assumptions about forces and their distribution, I identify morphological features that cause orientation and contribute to stability once oriented. By comparing the forces on an oriented and unoriented clam, I infer the function of orientation. In addition to measuring velocities, forces, and pressures, I experimentally manipulated the weight distribution of a *D. variabilis* clam and observed the resulting changes of the clam's motion in flow.

Materials and Methods

Backwash speed

On a North Carolina beach with a slope of 0.1, where *Donax variabilis* occurs, buoyant plastic beads (1 cm diameter) were dropped into the backwash and photographed at an exposure of 1/4 s. On the photographs, beads appear as streaks, and streak length was calibrated using a series of stakes planted in the beach at 1-m intervals along a transect perpendicular to the beach at the same location. It was assumed that the plastic beads moved at the same speed as the backwash. Error in the velocity calculated was determined by a propagation of errors analysis using estimated errors in the shutter speed and distance measures (Ellers, 1988).

Force distribution, due to flow, on an oriented and unoriented clam

To investigate the influence of shape and orientation on flow forces experienced by *D. variabilis* clams, the distribution of forces acting normal to the surface of a clam, and their associated moments, were determined. Local force normal to a surface equals local pressure multiplied by local surface area perpendicular to the force. Moment of a local force about the pivotal point equals the vector cross-product of location and force (location is a distance vector from the pivotal point to the force). Thus pressures, areas, and locations must be measured.

The pressure distribution was estimated by measuring pressure at many points on the surface of a scaled model clam that was 5 times larger than a real *D. variabilis* clam. A model was used because direct measurement of the distribution of pressures on such small clams (maximum length of real clams = 3 cm) is not feasible. Pressure mea-

surements on the scale model were made in a wind tunnel. Flows relevant to clams on the beach were mimicked in the wind tunnel by maintaining dynamic similarity (constant Reynolds number, Re). Due to equivalence of Euler number in dynamically similar flows (Shames, 1982), forces on an object determined in air were translated to forces on that object in seawater using

$$F_c = F_m \frac{\mu_w^2 \rho_a}{\mu_a^2 \rho_w}$$

where F_c and F_m are the forces on the template clam and model, μ_w and μ_a are the dynamic viscosities of seawater and air, and ρ_w and ρ_a are the densities of seawater and air. Assuming 20°C for both air and seawater, the conversion was

$$F_c = 4.14 F_m$$

The model was carved according to measurements of the shape of the outside of the left valve of a 2.2-cm-long *D. variabilis* clam. The valve was attached to a horizontal plane above which the valve protruded. A spring-loaded displacement gage measured vertical distance, and calibrated drives were used to determine horizontal coordinates. This apparatus gave a grid of 3-dimensional coordinates outlining the valve's shape. The grid had a vertical measurement every millimeter in both horizontal directions with more closely spaced measurements taken in regions where vertical measurements changed too rapidly with horizontal distance.

A model 5 times larger than the measured valve and a mirror-image right valve were fabricated to within ± 0.5 mm (maximum error) of the scaled measurements of shape. When the two valves were attached to each other, a hollow space existed inside. Eighty holes were drilled in the model and a hollow steel pipe, 0.26 mm in external diameter, was attached to the middle of the posterior end such that the interior of the pipe led to the hollow inside the model. The holes were covered with tape; during pressure measurements, one hole at a time was uncovered till pressure at all holes had been measured.

The model was placed on the floor of a large wind tunnel (Tucker and Parrott, 1970). The pipe that protruded from the posterior end of the model was attached to a pressure sensor *via* rubber tubing. On the other side of the pressure sensor was another rubber tube that connected to a reference hole in a horizontal flat plate located in and parallel to mainstream flow (40 cm above the tunnel floor). The reference hole was 1 mm in diameter and 0.1 m downstream of the leading edge of the plate. Measurement is made of the difference between the reference pressure at the hole in the plate and the pressure at the open hole on the model clam. The same apparatus was previously used to measure pressures on model squids (Vogel, 1985). The pressure signal was digitized (12-bit)

into a computer for data analysis. For each hole, 30 replicate pressure measurements were taken.

In the wind tunnel, the model was positioned on its left side at a tilt that was within $\pm 3^\circ$ of the angle at which a live clam lies in seawater. In seawater, a live clam lies with the plane of symmetry (between the right and left valves) at an angle of $11 \pm 2^\circ$ to the horizontal in both the anterior-posterior direction and the dorsal-ventral direction. These angles were measured using a protractor, from a photograph of a live clam lying on the bottom of a transparent aquarium filled with seawater. The photograph was taken from 10 m away to minimize distortion due to perspective.

Six sets of pressure measurements were made. Two were made at a mainstream air speed of 2.6 m s^{-1} , the equivalent of 0.91 m s^{-1} in 20°C seawater. The other four sets were made at a wind speed of 4.6 m s^{-1} , the equivalent of 1.6 m s^{-1} in 20°C seawater. Orientations of the model in the faster flows were (1) anterior end upstream, (2) posterior end upstream, (3) ventral edge upstream, and (4) dorsal edge upstream. In the slower flows, only orientations (1) and (3) were tested.

When the anterior end was upstream, the dorsal edge was at 3.6° ($< \pm 3^\circ$ error) counter-clockwise (when looking from above) relative to mainstream flow. The other orientations were rotated 90° , 180° , and 270° with respect to that position.

Three perpendicular components of force are obtained by multiplying pressures by projected areas perpendicular to each component (with appropriate sign conventions). Projected areas were obtained from six photographs, parallel to all sides of a cube, of the model taken from a distance of 15–20 m with a 200-mm lens (the large distance minimizes systematic distortion of area resulting from perspective). Area was measured by weighing areas cut out of the photographs and also, for comparison and estimation of errors, by digitizing the areas with a digitizing tablet and a computer. Error in the area measurement, including bias from area distortion (the difference between the area of calibration square centimeters in front of and behind the clam model) and imprecision (estimated as the standard deviation of repeated measurements), was always less than $\pm 10\%$. For the moment calculations, the 3-dimensional location coordinates of all holes were also measured from these photographs. Location was measured with an error less than $\pm 7\%$. The (0,0,0) coordinate was placed at the pivotal point (the point at which the shell touches the ground).

A propagation of errors analysis was performed according to standard formulas (see p. 28 in Schulz, 1945; Ku, 1969). Errors propagated through the moment, and force calculations were the measured standard deviation of pressure at each hole, and an assumed $\pm 10\%$ of the area and $\pm 7\%$ of the distance at each hole.

Another source of error, not expressed in the propagation analysis, is the contribution of tangential forces acting on the surface of the clam. Total force is the sum of forces normal and tangential to the surface, but only the normal forces are measured here. Tangential forces can reasonably be ignored because, for non-streamlined objects at the relevant Re values, tangential forces are relatively small. For instance, friction drag (due to components of tangential forces) is much smaller than pressure drag (due to components of normal forces). For a cylinder perpendicular to flow, pressure drag is 87% and 97% of total drag at $\text{Re} = 10^3$ and 10^4 , respectively (Vogel, 1981). Also, for ellipsoidal shapes, with length-to-diameter ratios ranging from 2:1 (long axis parallel to flow) through 1:1 (sphere) to 1:2 (long axis perpendicular to flow), pressure drag ranges from $>80\%$ up to $>95\%$ of total drag, respectively, at $\text{Re} = 7 \times 10^4$ (Hoerner, 1965). These results apply at subcritical Re values; *i.e.*, in flows in which there is separation of flow on the object. Flow around clams is comparable since (i) flow separates on these clams (observed using dyes and inferred from pressure measurements: see results), and (ii) clams have length-to-diameter ratio of 2:1 or 1:2 depending on orientation, and (iii) measurements were made at $\text{Re} = 1.9$ and 3.4×10^4 . Thus, components of normal forces measured here will tend to underestimate drag forces, perhaps by as much as 5%–20%.

The relative size of the clam and the boundary layer also affects pressure measurements; thus the velocity distribution existing in the wind tunnel under experimental conditions is given for comparison. It was measured at a mainstream wind of 2.6 m s^{-1} using a Pitot tube and the same pressure sensor as was used for the clam. Velocity was calculated from

$$\Delta p = \frac{\rho U^2}{2}$$

where Δp is the pressure difference between the static and dynamic openings of the Pitot tube, ρ is the density of the medium, and U is the velocity of the flow at that point (Vogel, 1981).

Density, weight and size of D. variabilis and density of other Bivalvia

Live *D. variabilis* specimens of a range of sizes were weighed while they were immersed in water and in air. A formula based on Archimedes Principle was used to calculate the density, ρ_D , of *D. variabilis*.

$$\rho_D = \frac{\rho_s W_A}{(W_A - W_W)}$$

where ρ_s is the density of seawater, W_A is the weight of the clam in air, and W_W is the weight of the clam in sea-

water. The general shape of these clams is also relevant. Using calipers, basic dimension measurements were made of the anterior–posterior, ventral–dorsal, and left–right distances on the same clams.

The densities of other bivalve species, chosen haphazardly on North Carolina beaches, were determined in the same way (three specimens each of seven species were measured). Specimens of the same size as a large individual of *D. variabilis* (2–3 cm long) were used to minimize potential allometric effects on the comparison.

Density, weight distribution, and size effects on orientation

Motions of *D. variabilis* shells of various sizes with experimentally altered density and weight distribution were qualitatively observed in steady flows up to 60 cm s^{-1} in a recirculating flow tank. Tendency to orient and the flow speed at which orientation occurred were noted.

Weight distribution was altered by placing Plasticene in the posterior end and an air bubble in the anterior end (and *vice versa*), of empty *D. variabilis* shells. (Altering weight distribution also unavoidably altered density.) Density was altered by completely filling empty *D. variabilis* shells with candle wax, Silicone rubber or Plasticene; the resulting densities of filled shells were 1.5, 1.7 and $2.0 (\times 10^3 \text{ kg m}^{-3})$, respectively. (Altering density unavoidably alters weight distribution slightly.) Shells were placed in flow with four initial orientations: ventral, dorsal, posterior, or anterior edges upstream.

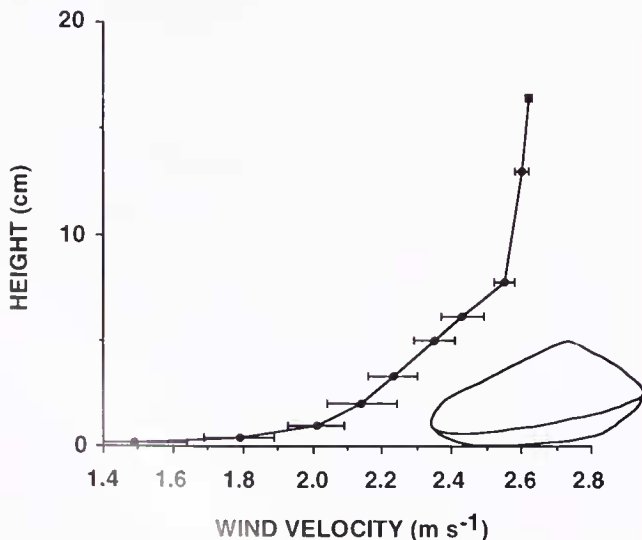


Figure 3. The wind-speed distribution in the tunnel in which pressure measurements on the clam model were made. The mainstream velocity was equivalent to 0.91 m s^{-1} in seawater. The clam was well inside the boundary layer, and is shown for scale (it was not in the tunnel while the speed distribution was measured). Error bars show 1 SD.

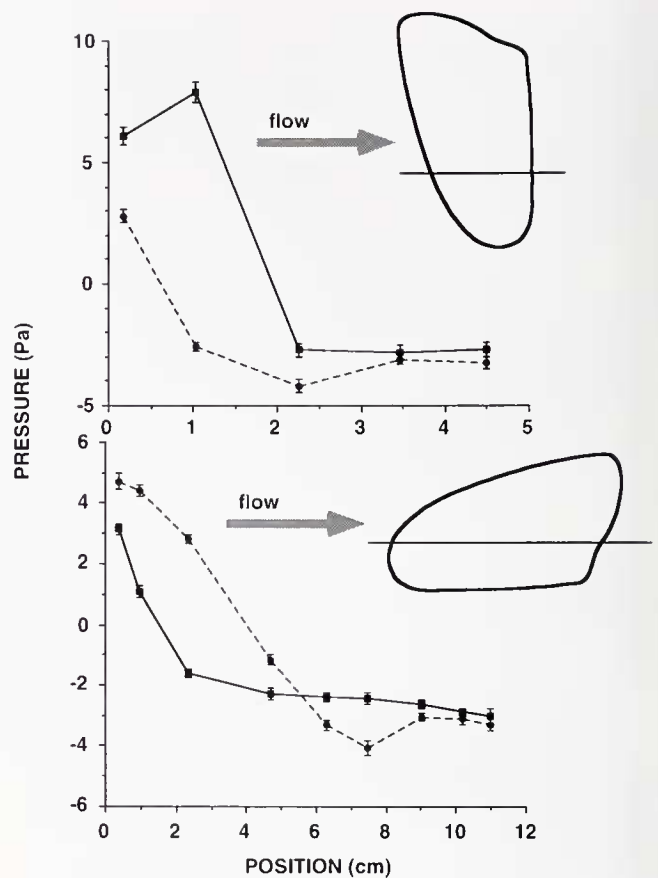


Figure 4. Pressure measurements taken along transects with the clam oriented with the ventral edge upstream and the anterior end upstream. Positive pressures indicate forces acting inward normal to the surface; negative ones indicate outward forces. Dashed line joins upper (right) valve measurements; solid line joins lower (left) valve measurements. Error bars are 1 SD. (For comparison, mainstream wind velocity was 4.6 m s^{-1} , which corresponds to a dynamic pressure of 13 Pa.)

Results

Backwash speed

The average speed of 33 beads was $0.76 \pm 0.20 \text{ m s}^{-1}$ standard deviation. Speed ranged from 1.1 to 0.38 m s^{-1} . Inaccuracy bounds ($>95\%$ confidence intervals) from a propagation of errors estimate are $\pm 11\%$ for the higher speeds, and $\pm 26\%$ for the lower speeds.

Force distribution due to flow on an oriented and unoriented clam

In the wind tunnel, a clam model was located within the gradient of speeds of the boundary layer (Fig. 3). The model's shape altered the velocity distribution around it, which caused pressures on the model. Observed pressure distributions (Fig. 4) are similar to those typical of a bluff body such as a cylinder perpendicular to flow in that, first,

on the upstream side, pressures were high (causing forces pushing downstream); second, partway downstream, pressures became negative (causing outward forces) as flow sped up around the clam; and third, at the downstream end, pressures did not recover (did not become positive as they would have done in an ideal fluid or on a streamlined shape), thus giving rise to pressure drag and signaling separation of flow on the model.

Unlike the pressure distribution on a cylinder, however, time-averaged pressures on the upper and lower surfaces were unequal and resulted in lift. Different characteristic pressure distributions were observed when the anterior end was upstream, as in other orientations. When the ventral edge was upstream, the upper valve always experienced lesser pressures than the lower valve, thus giving rise to upward lift. In contrast, when the anterior end was upstream, the pressure was alternately lesser on the lower and then on the upper surface as flow proceeded downstream: forces from these pressures summed to downward lift.

The overall effects of the pressure distributions in oriented and unoriented clam models are summarized by the resulting forces and moments (Table I). Lift was downward when the anterior end was upstream and upward when the model was in any other orientation. Drag when oriented with the anterior end upstream was less than drag in any other orientation.

When oriented with the anterior end upstream, the model clam experienced a moment tending to force rotation of the anterior end into the sand (Table I; Fig. 5). In other orientations there was also an analogous moment tending to push the anterior end into the sand. Orientation towards the stable position with the anterior upstream may be enhanced by such a moment because it tends to cause tilting; tilting moves the pivotal point anteriorly,

thus increasing rotational moments about the vertical, pivotal z -axis.

Even without such tilting, when oriented with the ventral, dorsal, or posterior ends upstream, there were large moments tending to rotate the clam model about the vertical axis and towards an orientation with the anterior end upstream (Fig. 6). In contrast, when the anterior end was upstream, the clam model experienced much smaller moments about the vertical, z -axis. The anterior upstream orientation is rotationally stable.

Density, weight, and size of D. variabilis and density of other Bivalvia

D. variabilis is one of the densest bivalves measured (Table II). Size and weight are described for 20 specimens. The (ventral–dorsal distance) = 0.51 (anterior–posterior distance) + 0.081, $r^2 = 0.995$; and the (left–right distance) = 0.36 (anterior–posterior distance) + 0.028, $r^2 = 0.98$, with all distances in centimeters. The anterior–posterior distances ranged from 0.51 to 2.3 cm, and corresponding weights ranged between $7.6 \cdot 10^{-5}$ and $6.8 \cdot 10^{-3}$ N. The (weight in seawater) = $6.2 \cdot 10^{-4}$ (anterior–posterior distance)^{2.9}, $r^2 = 0.99$, with weight in N and distance in centimeters.

Density, weight distribution, and size effects on orientation

The tendency to orient with the anterior end upstream in flow is affected by a combination of density, weight distribution, and size (Table III). When shells oriented, they rotated around a vertical axis through the pivotal point and did so while either sliding downstream or remaining at their original location. Weight distribution affected the location of the pivotal axis: the more relatively

Table I

Forces and moments due to flow-induced normal forces at two speeds in seawater (converted from wind tunnel measurements using dynamic similarity)

End Upstream	Speed $m \cdot s^{-1}$	Drag $\times 10^{-4}$ N	Lift _H $\times 10^{-4}$ N	Lift _V $\times 10^{-4}$ N	M _x $\times 10^{-6}$ Nm	M _y $\times 10^{-6}$ Nm	M _z $\times 10^{-6}$ Nm
Anterior	0.91	72 ± 2.8	-39 ± 2.9	-22 ± 4.6	16 ± 2.6	-3.0 ± 3.3	14 ± 2.6
Anterior	1.6	310 ± 10	-130 ± 11	-94 ± 17	17 ± 11	-31 ± 14	49 ± 10
Posterior	1.6	600 ± 15	-330 ± 17	470 ± 26	160 ± 22	570 ± 27	340 ± 17
Dorsal	1.6	960 ± 24	340 ± 19	810 ± 41	-220 ± 26	530 ± 24	140 ± 13
Ventral	0.91	200 ± 6.6	66 ± 6.2	54 ± 12	11 ± 7.8	65 ± 7.3	-88 ± 4.6
Ventral	1.6	560 ± 17	120 ± 14	500 ± 29	67 ± 17	270 ± 15	-240 ± 10

These measurements apply to a *D. variabilis* clam with an anterior–posterior distance of 2.2 cm. For comparison, this clam weights 61×10^{-4} N in seawater. The coordinate system used for the moments is right-handed* and the positive x -axis is downstream, the positive z -axis is up. Errors, determined by propagation of errors analysis, that approximate 1 SD are shown. Lift_H is horizontal lift; Lift_V is vertical lift; M_x is the moment about the x -axis; M_y is the moment about the y -axis; M_z is the moment about the z -axis.

* Sign convention for moments: if you point your right-hand thumb in the positive direction along the axis about which a moment is tending to cause rotation, then a positive moment tends to cause rotation in the direction that your fingers are pointing. A negative moment tends to cause rotation in the opposite direction.

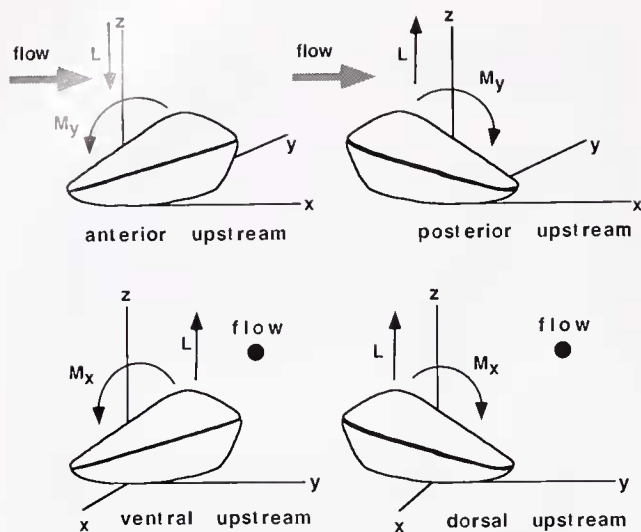


Figure 5. Vertical lift forces and moments tending to tilt a clam's anterior end downward in flow in four different orientations. (Magnitudes not to scale.) The dot indicates flow out of the page; the x -axis is positive downstream. For other symbol and axis definitions see Table I.

heavy the anterior end, the closer the pivotal axis was to the anterior end and the more likely the clam was to orient with the anterior end upstream. If the posterior end was sufficiently heavy, then the pivotal axis lay closer to the middle and no orientation was stable. Denser or larger clams oriented with the anterior end upstream at higher flow speeds. The densest filled shells tested did not orient with the anterior upstream at any of the tested speeds.

Discussion

Morphological causes of passive orientation to a rotationally stable position

A clam orients with the anterior end upstream because moments about a vertical axis through the pivotal point tend to rotate the anterior end upstream (Table I; Fig. 6). Once the anterior end is upstream, the moment about that vertical axis is smaller. Further, rotational moments reverse direction if a clam rotates past that position; thus, once the anterior end is upstream, it tends to stay there.

Larger moments that occur when posterior, ventral, or dorsal edges are upstream are a combined result of the wedge-like shape of *D. variabilis* and the location of the pivotal point. The wedge-like shape creates larger moments by having unequal projected areas, subject to pressure drag, on either side of the vertical axis through the pivotal point. Likewise, if the pivotal point is located close to one end of the clam, then unequal projected areas exist on either side of the vertical axis.

The location of the pivotal point is determined both by a clam's weight distribution and by forces from flow.

Forces from flow tilt a clam such that the anterior end is pushed into the sand (Table I; Fig. 5), which moves the pivotal point anteriorly. Tilting thus further increases the projected area on one side of the pivotal axis and increases the moment, tending to cause orientation with the anterior end upstream. Experimentally changing the tilt by changing the weight distribution (using an air bubble and Plasticsene in opposite ends) either enhanced or prevented orientation. When the posterior end was heavier and tilted down, the pivotal point moved posteriorly and orientation was prevented because the projected area that gives rise to orienting moments was nearly equal on either side of the vertical axis. Conversely, when the anterior end was heavier and tilted downward, orientation occurred in the flow tank even in relatively slow flow.

In general, orientation depends on flow speed. A minimum flow speed is required because static friction between clam and sand prevents rotation below critical forces and speeds. Equations modeling force balances just prior to rotation show that larger or denser clams require higher flow speeds to start rotating (Ellers, 1987, 1988). Similarly, experiments showed that higher minimum flow speeds are required for orientation of larger and denser shells (Table III).

Density is also crucial in keeping the pivotal point on the ground. If a shell is too light, upward lift can temporarily raise the shell, which results in tumbling rather than orientation. For example, less dense bivalves, such

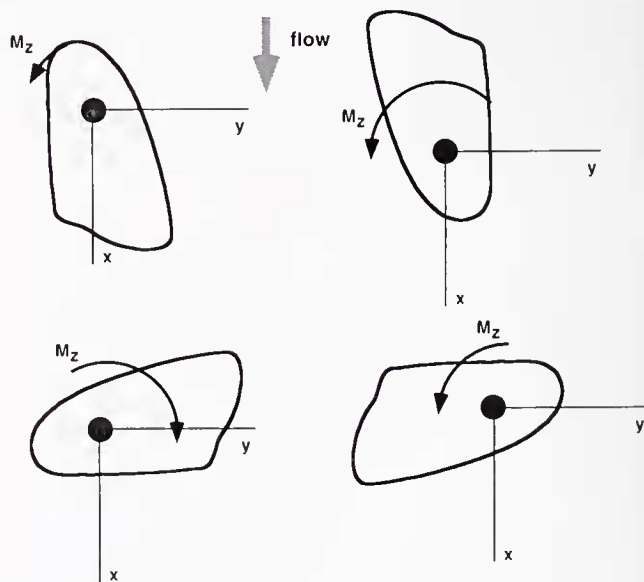


Figure 6. Moments tending to rotate a clam about the vertical, z -axis through the pivotal point. Four initial orientations are shown. Moments tend to rotate a clam towards a position with the anterior end upstream (upper left). That orientation is stable because rotational moments are nearly zero and rotational moments change sign (and direction) if a clam rotates past that orientation. (Magnitudes not to scale.)

Table II

Densities of several species of clams found on North Carolina beaches; most bivalve species are less dense than *D. variabilis*, which has a density of 1.65 ± 0.5 SD, $n = 20$

Species	Density $\times 10^3$ kg m ⁻³
<i>Chione cancellata</i>	1.66
<i>Mercenaria mercenaria</i>	1.54
<i>Spisula raveneli</i>	1.47
<i>Macrocallista nimbosa</i>	1.53
<i>Divaricella quadrisculata</i>	1.40
<i>Tellina iris</i>	1.26
<i>Tagellus plebeius</i>	1.17

as *Tellina iris* or *Tagellus plebeius*, tumbled when placed in backwash. Thus, the high density of *D. variabilis* among bivalves (Table II), may be crucial for orientation during swash-riding. A *D. variabilis* clam is in danger of being lifted off the sand in flows from waves: the underwater weight of a clam, 2.2 cm long, is less than its upward lift when it is oriented with the posterior, ventral, or dorsal edge upstream (Table I) in a flow of 1.6 m s⁻¹. In contrast, at 0.91 m s⁻¹, this clam is slightly heavier than the lift it experiences; orientation to a stable position could occur.

Forces exerted on a *D. variabilis* clam at flow speeds encountered in backwash can be expected to cause orientation: observed speeds in the backwash averaged 0.76 m s⁻¹, and 60% of the observed speeds were between 0.56 and 0.96 m s⁻¹. Indeed, these clams often orient in backwash (Fig. 2). Flow speeds of swash are usually higher, reaching a maximum of 3 m s⁻¹ even on shallow-sloped beaches (Bradshaw, 1982); thus forces exerted on *D. variabilis* at flow speeds encountered in swash can cause tumbling. Indeed, on a beach, clams often tumble in swash, usually orienting with the anterior end upstream when the swash slows as it reaches its maximum beachward position, or in slower flow in the backwash.

These measurements and observations suggest that the shape and density of *D. variabilis* clams are a complex of morphological characters that act in concert and that are crucial in creating orientation in flow. Further, there is a range of flow speeds in which *D. variabilis* clams can rotate to a stable orientation, and speeds in that range are common on beaches on which these clams live.

Consequences of orientation: a stable, slower ride

When a *D. variabilis* clam is oriented with the anterior end upstream, it experiences less drag than in any other orientation (Table I). Furthermore, it experiences downward lift. Lower drag is primarily attributable to the lower projected surface area exposed to pressure drag when a clam's long axis is parallel to flow. Downward lift is pri-

marily due to the downward tilt of the anterior end of the clam relative to the posterior end, which effectively creates a negative angle of attack relative to flow. Lower drag and downward lift result in a stable, slower ride.

Lower drag resulting in slower speed relative to the substratum may seem initially counterintuitive because drag is most commonly encountered as a force that impedes motion. During swash-riding, however, drag is a force that propels a clam. A higher drag results in a sliding speed more nearly water speed, and therefore a greater ground speed. Conversely, lower drag and downward lift (higher friction with the ground) cause slower speeds of swash-riding relative to the substratum.

During slower, stable sliding with the anterior end upstream, the foot, which protrudes from the anterior end, has a better chance of achieving a foothold than if the clam were tumbling, rotating, or oriented any other way. After gaining a foothold, the sand upstream of a clam tends to get scoured out (Fig. 2), which assists a clam in digging into the sand. On a beach, dead shells oriented with the anterior end upstream were sometimes observed to sink passively into the scoured sand just upstream of their shells. Thus, orientation with the anterior end upstream enhances a clam's ability to stop moving and to burrow into the sand after a swash-ride.

A clam's ability to maintain position on the beach or to make net shoreward progress during shoreward migration depends on its being able to establish a foothold before being washed out to sea. Gaining a foothold while the backwash is flowing is therefore crucial. Orientation with the anterior end upstream, with its concomitant reduced drag and downward lift, may be the decisive factor in making migration by swash-riding possible.

Table III

Qualitative observations of the effects of weight distribution, density, and size on the tendency of *D. variabilis* shells to orient passively with the anterior end upstream

Variable	Level	Final Orientation in Flow
Weight distribution	Light anterior	No orientation
	Light posterior	Anterior upstream always
Density	1.5×10^3 kg m ⁻³	Anterior upstream usually
	1.7×10^3 kg m ⁻³	Anterior upstream occasionally
	2.0×10^3 kg m ⁻³	No orientation
Size*	2.2 cm	Anterior upstream above 40 cm s ⁻¹
	1.5 cm	Anterior upstream above 30 cm s ⁻¹
	1.2 cm	Anterior upstream above 25 cm s ⁻¹

Shells were experimentally altered as indicated and were placed in a flow tank with one of the initial orientations (anterior, posterior, ventral, or dorsal edge upstream). Max. flows tested were 60 cm s⁻¹.

* Numbers shown are for filled shells of density 1.5×10^3 kg m⁻³.

Morphological and behavioral control of swash-riding

That shape can affect movement of clam-like objects in waves has been demonstrated previously (Lever, 1958; Lever *et al.*, 1961, 1964, 1968). Wave-induced, passive, net movement of many thousands of manufactured model *Donax vittatus* valves were observed over one tidal cycle. Right valves were swept seaward, whereas left valves remained on the beach; less dense valves moved further than more dense ones; larger shells remained on the beach longer than smaller ones. Thus, net passive movement of valves by waves depends on density, size, and shape. Likewise, the movements of whole, live clams also depend on these variables. *D. variabilis* clams control where waves move them by using a combination of behavior and a complex of morphological characters: the wedge-like shape, high density, and anteriorly located pivotal point.

A *D. variabilis* clam can modulate its speed on the beach relative to the speeds of the swash and backwash occurring under a range of wave conditions. On days with only small waves and slow swash and backwash speeds, clams protract foot and siphons (pers. obs.), thus increasing drag and clam speed by exposing more area to flow. On days with higher waves, clams keep foot and siphons retracted, decreasing their speed relative to flow. If flow speeds are sufficiently high to cause orientation, a clam orients with the anterior end upstream, which reduces drag and thus again reduces clam speed relative to flow speed. If flow speeds are so high that the clam tends to tumble before it can orient, then the clam tumbles in flow and moves nearly at flow speeds until the flow slows down, as it usually does in the backwash. Once the flow is sufficiently slow for orientation, a clam can regain a foothold.

Ecological and evolutionary consequences

Net movement in waves, the number of swash-rides required for migration, and hence the energy cost of migration (Ansell and Trueman, 1973), depend on both the prevailing wave conditions and the shape and behavior of a swash-riding clam. Flow speeds from waves typically depend on beach structure and wave conditions. Whether *D. variabilis* clams can live on a given beach will depend on the prevalence of suitable flow speeds on the beach. Flow speeds must typically be fast enough to overcome friction between clam and sand, but slow enough that lift-off does not occur in the backwash.

The functional morphology of swash-riding thus suggests that the swash-riding performance of a *Donax* species should be related to typical flows on the beaches on which it lives. An intriguing comparison species is the largest (7 cm long) *Donax* species, *Donax serra*, which swash-rides but migrates on a semilunar cycle (Donn *et al.*, 1986) rather than a tidal cycle. Zonation patterns of different populations of *D. serra* were found to be statistically ex-

plained by the morphological characters weight, surface area, and elongation; populations found higher in the intertidal had thicker valves and higher density than those found lower in the intertidal (Donn, 1990).

Similarly, the ecology of sandy beaches may depend on the flow regime of swash and backwash. The physical environment, described by wave-regime parameters, was found to control species richness of sandy beach fauna (McLachlan *et al.*, 1993). Body size and means of locomotion (such as swash-riding) were suggested as important parameters in determining the extent to which organisms were able to live on beaches as the swash "climate" became harsher.

The functional morphology of swash-riding clams also suggests characters that may have been important in the evolution of swash-riding in donacid bivalves. Since swash-riding is enabled by high density, a wedge-like shape, and an anteriorly located pivotal point, evolution of these characters is predicted to be correlated with swash-riding. A large range of donacid species inhabiting a range of beach types exists in the world. Independent contrasts methods (Harvey and Pagel, 1991) and morphological comparisons using functional morphospaces (Ellers and Telford, 1991; Moore and Ellers, 1993) could be applied to test whether these characters are evolutionarily correlated with swash-riding.

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Literature Cited

- Ansell, A. D., and E. R. Trueman. 1973. The energy cost of migration of the bivalve *Donax* on tropical sandy beaches. *Mar. Behav. Physiol.* 2: 21-32.
- Bradshaw, M. 1982. Bores and swash on natural beaches. *Coastal Studies Unit Technical Report No. 82/4* Coastal Studies Unit, Department of Geography, The University of Sydney, Sydney, NSW, Australia.
- Donn, T. E., Jr. 1990. Morphometrics of *Donax serra* Röding (Bivalvia: Donacidae) populations with contrasting zonation patterns. *J. Coastal Res.* 6: 893-901.
- Donn, T. E., Jr., D. J. Clarke, A. McLachlan, and P. du Toit. 1986. Distribution and abundance of *Donax serra* Röding (Bivalvia: Donacidae) as related to beach morphology. I. Semilunar migrations. *J. Exp. Mar. Biol. Ecol.* 102: 121-131.
- Ellers, O. 1987. Passive orientation of benthic animals in flow. Pp. 45-68 in *Signposts in the Sea, Proceedings of a Multidisciplinary*

- Workshop on Marine Animal Orientation and Migration*, W. F. Herrnkind and A. B. Thistle, eds. Dept. of Biological Science, Florida State University, Tallahassee.
- Ellers, O. 1988. Locomotion via swash-riding in the clam *Donax variabilis*. Ph.D. Dissertation, Duke University, Durham, NC.
- Ellers, O. 1995a. Behavioral control of swash-riding in the clam *Donax variabilis*. *Biol. Bull.* 189: 120-127.
- Ellers, O. 1995b. Discrimination among wave-generated sounds by a swash-riding clam. *Biol. Bull.* 189: 128-137.
- Ellers, O., and M. Telford. 1991. Forces generated by the jaws of clypeasteroids (Echinodermata: Echinoidea). *J. Exp. Biol.* 155: 585-603.
- Harvey, P. H., and M. D. Pagel. 1991. *The Comparative Method in Evolutionary Biology*. Oxford University Press, Oxford. 239 pp.
- Hoerner, S. F. 1965. *Fluid-Dynamic Drag*. S. F. Hoerner, 2 King Lane, Greenbriar, Brick Town, NJ 08723.
- Jacobson, M. K. 1955. Observations on *Donax fossor* Say at Rockaway Beach, New York. *Nautilus* 68: 73-77.
- Ku, H. H. 1969. Notes on the use of propagation of error formulas. Pp. 331-263 to 341-273 in Chapter 5, Section 2 of *Precision Measurements and Calibration, Statistical Concepts and Procedures*, Special Publication 300, Vol. 1, H. H. Ku., ed. U.S. Dept. of Commerce, National Bureau of Standards.
- Lever, J. 1958. Quantitative beach research I. The "left-right phenomenon": sorting of lamellibranch valves on sandy beaches. *Basteria* 22: 21-51.
- Lever, J., M. van den Bosch, H. Cook, T. van Dijk, A. J. H. Thiadens, and R. Thijssen. 1964. Quantitative beach research III. An experiment with artificial valves of *Donax vittatus*. *Neth. J. Sea Res.* 2: 458-492.
- Lever, J., A. Kessler, A. P. van Overbeeke, and R. Thijssen. 1961. Quantitative beach research II: The "hole effect": a second mode of sorting of lamellibranch valves on sandy beaches. *Neth. J. Sea Res.* 1: 339-358.
- Lever, J., and R. Thijssen. 1968. Sorting phenomena during transport of shell valves on sandy beaches studied with the use of artificial valves. *Symp. Zool. Soc. Lond.* 22: 259-271.
- McLachlan, A., E. Jaramillo, T. E. Donn, and F. Wessels. 1993. Sandy beach macrofauna communities and their control by the physical environment: a geographical comparison. *J. Coastal Res.* Special Issue 15: 27-38.
- Moore, A. M. F., and O. Ellers. 1993. A functional morphospace, based on dimensionless numbers, for a circumferential calcite stabilizing structure in sand dollars. *J. Theor. Biol.* 162: 253-266.
- Mori, S. 1938. Characteristic tidal rhythmic migration of a mussel, *Donax semigranosus* Dunker, and the experimental analysis of its behaviour at the flood tide. *Dobutsugaku Zasshi*. [=Zool. Mag. (Japan)] 50: 1-12.
- Schulz, G. 1945. *Formelsammlung zur praktischen Mathematik*, Göschen Band 1110. W. de Gruyter, Berlin.
- Shames, I. H. 1982. *Mechanics of Fluids*. McGraw Hill Book Co., New York.
- Tiffany, W. J. III. 1971. The tidal migration of *Donax variabilis* Say (Mollusca: Bivalvia). *Veliger* 14: 82-85.
- Tueker, V. A., and G. C. Parrott. 1970. Aerodynamics of gliding flight in a falcon and other birds. *J. Exp. Biol.* 52: 345-367.
- Vogel, S. 1981. *Life in Moving Fluids*. Princeton University Press, Princeton, NJ.
- Vogel, S. 1985. Flow-assisted shell reopening in swimming scallops. *Biol. Bull.* 169: 624-630.
- Wade, B. 1967. Studies on the biology of the West Indian Beach clam, *Donax denticulatus* Linné. 1. Ecology. *Bull. Mar. Sci.* 17: 149-174.